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Too close and too far: quantifying black rhino displacement and location error during research

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Observer impacts on animal behaviour concern conservation managers and researchers of critically endangered species, like black rhino (*Diceros bicornis*). Repeated observations are sometimes necessary, but may distress and displace animals. Information from more remote observations using radio-triangulation is limited and includes larger measurement errors. We investigated the influence of observer visits on average daily displacement by 14 black rhinos in Hluhluwe-iMfolozi Park, South Africa, and the accuracy of triangulated locations with increasing observer distance and the time to complete bearing sets. Fortnightly observer visits for 34 months that often disturbed rhino (52% of visits) had an insignificant impact on daily movements. However, increasing observer distance from rhino, and the time taken to triangulate, were both significant explanations of rhino location error. We recommend that measures to quantify and minimize observer influence become standard monitoring protocol and that bearings for radio-triangulation of black rhino locations occur from <1 km (not >2 km), and be completed within 30 minutes. Reporting measures for spatial error and observer influence permit the development of objective thresholds for data inclusion to improve radio-telemetry data and inter-study comparisons of black rhino range studies.

Key words: observer disturbance, radio-telemetry, radio-triangulation, home range, *Diceros bicornis minor*, Hluhluwe-iMfolozi Park, rhinoceros, conservation management.

INTRODUCTION

Accurate measures of animal location and movement are fundamental to the monitoring of individuals and populations, and in conservation planning and management towards species recovery. Radio-telemetry has been integral to wildlife monitoring for several decades (i.e. >75% of home range studies have used radio-telemetry; Laver & Kelly, 2008) as it facilitates knowing the identity and location of free-ranging animals. Notwithstanding its value, radio-telemetry is not without limitations. Ground-based radio-tracking to observe and locate an animal may subject it to repeated human disturbance. Disturbance can be reduced by radio-signal triangulation from greater distances but it is prone to greater location error than direct sightings (White & Garrot, 1990). Quantifying the influence that observers have on animal displacement and the location error from triangulations

with increasing distance from animals would provide greater confidence in ecological studies that use radio-telemetry and assist in balancing concerns about animal disturbance and location error, but these are rarely achieved (Saltz, 1994).

Conservationists are increasingly concerned about human disturbance effects on wildlife and their management (Frederick & Colpopy, 1989; Carney & Sydeman, 1999; Beale & Monaghan, 2004; Kolowski & Holekamp, 2008; Crosmar, Valeix, Fritz, Madzikanda & Cote, 2012; Selier, Slotow & Di Minin, 2015). Disturbance by researchers and tourists has been implicated in the reduced breeding performance and altered behaviour of several bird (e.g. Adele, *Pygoscelis adeliae*, and Magellanic Penguins, *Spheniscus magellanicus*; Puffins, *Fratercula arctica*; Culik & Wilson, 1995; Rodway, Montevecchi & Chardine, 1996; Walker, Boersma & Wingfield, 2005) and mammal species (e.g. impala, *Aepyceros melampus*, lions, *Panthera leo*, and whales, *Odontocetes* and *Mysticetes* spp.; Matson, Goldizen & Putland, 2005; Hayward &

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Hayward, 2009; Senigaglia *et al.*, 2016). If unaddressed, these concerns could undermine the contribution that research and tourism bring to species conservation (Rodway *et al.*, 1996; Carney & Sydesman, 1999; Carey, 2009).

Human presence induces vigilance, alarm and escape responses (displacement) in the critically endangered (Emslie, 2015) black rhinoceros (*Diceros bicornis*) (hereafter rhino) (Schenkel & Schenkel-Hulliger, 1969; Owen-Smith, 1987; Berger & Cunningham, 1995; Göttert, 2011; Plotz, 2014). There is concern that human disturbance may displace black rhinos from preferred habitat (Berger & Cunningham, 1995; Beytelli, 2010; Göttert, 2011; Odendaal, 2011), but it is not known what impact regular monitoring has on their spatial behaviour. Black rhinos are typically monitored by obtaining direct sightings of individuals (Plotz, 2014), but this method can often disturb the focal animal because the dense vegetation in which black rhinos are found necessitates proximity to view the animal (e.g. <50m; Owen-Smith, 1988; Plotz, 2014). Indeed, the commonly used ear-notching technique for rhino identification encourages observers to disturb the animal because vigilant rhinos face the observer and present their ears forward (Amin *et al.*, 2006) – a posture allowing their notching pattern to be clearly seen (Hitchins, 1990). Black rhinos will typically run once they confirm that people are near (e.g. human scent; Owen-Smith, 1987, 1988; Plotz, 2014). Studies of black rhinos have yet to address the impact that observers might have on their locations and movement.

Radio-telemetry is being replaced by GPS satellite technologies for most wildlife (e.g. satellite collars on savanna elephants, *Loxodonta africana*; Thomas, Holland & Minot, 2008) but its successful deployment on black rhinos has been delayed through issues with overheating, unreliable signal transmission and attachment-related injuries such as lesions and tissue damage (e.g. from both neck and ankle collars; see Alibhai & Jewell, 2001a, b). Researchers, therefore, continue to rely on horn-implant VHF radio transmitters (Pienaar & Hall-Martin, 1991; Shrader & Beauchamp, 2001) for regular monitoring of black rhinos as they have proved to be robust to the challenges of rhinos and their habitat (e.g. Morgan, Mackey & Slotow 2009; Göttert, Schöne, Zinner, Hodges & Böer, 2010; Odendaal-Holmes, Marshall & Parrini, 2014; Plotz, Grecian, Kerley & Linklater, 2016).

Although triangulation from greater distances

may be the preferred way of reducing disturbance of radio-monitored animals, the technique is susceptible to a number of measurement errors (Macdonald & Amlaner, 1979). Bearings are inherently imprecise, especially due to radio-signal reflection and bearing bias (White & Garrott, 1990), increasing observer distance from the signal, and animal movement during triangulation (Macdonald & Amlaner, 1979; Lee, White, Garrott, Bartman & William-Alldredge, 1985; Harris *et al.*, 1990; Schmutz & White, 1990; Saltz, 1994).

In this study, we describe the effects that observers and radio-triangulation error have on black rhino movements and location estimates. This study aims to address questions about the impact of intensive monitoring for research on rhino populations and motivate improvements in black rhino location and movement studies using radio-triangulation.

STUDY AREA AND POPULATION

Huhluwe-iMfolozi Park (HiP) (28°0' to 28°25'S, 31°42' to 32°0'E) is a 960 km² fenced, semi-arid and mild-temperate South African reserve. Annual rainfall is largely seasonal (October to March) and decreases with latitude from 990 to 635 mm over steep to gentle hill-country terrain ranging from 450 to 60 m a.s.l. Average minimum winter temperatures are 13°C and average maximum summer temperatures are 33°C. The subtropical vegetation varies from grasslands to *Acacia* spp. woodlands and denser thickets dominated by broadleaf genera like *Euclea* and *Maytenus* (Balfour & Howison, 2001; Plotz, 2014; Plotz *et al.*, 2016).

HiP has the largest (c. 218; Clinning, Druce, Robertson, Bird & Nxele, 2009) surviving endemic population of south-central black rhino (*D. b. minor*) in Africa (Brookes & MacDonald, 1983) and undergoes annual black rhino harvesting (c. 5 to 8 % of the population) as it serves as a strategic donor (source) population for species rescue by reintroduction and restocking (e.g. Black Rhino Range Expansion Project, BRREP; Emslie, 2001; Linklater *et al.*, 2012; Plotz, 2014; Hayward *et al.*, 2017). Our experimental population consisted of 14 adult (>7 years; Law & Linklater, 2015) female rhinos who received horn-implanted radio transmitters (VHF) from March 2007 to October 2008 as part of a larger study of black rhino population dynamics (see Plotz & Linklater, 2009; Linklater *et al.*, 2010a; Plotz, 2014; Plotz *et al.*, 2016).

Descriptions of horn implant techniques and equipment are provided in Plotz *et al.* (2016). All

capture and study procedures were approved by Ezemvelo KwaZulu-Natal Wildlife (EKZNW) research department (Hill Top; permit no: ZC/101/01), Victoria University of Wellington Animal Ethics Committee (2007R2) and the Zoological Society of San Diego (IACUC number 169).

Although the procedure to immobilize and insert horn-implant radio-transmitters could increase the sensitivity that rhinos may have towards humans, this is less likely in HiP because almost all individuals in the population are immobilized several times over their lives for reasons other than inserting horn-implant radio-transmitters (e.g. ear notches where ear tissue is removed to create unique patterns for identification purposes and the insertion of short-range transponders under the skin; Hitchins, 1990). Moreover, female rhinos in HiP are likely to be immobilized several times over their breeding lives as the management policy is for the mothers of calves to be immobilized at the same time their calves receive their ear notches (Plotz, 2014).

METHODS

Obtaining direct sighting and radio-triangulated locations

Ground-based radio-telemetry was used to track and locate individual black rhinos either *via* direct observation (i.e. researcher at ≤ 50 m from rhino, estimated with a Leica Rangefinder CRF Range Master 1200) or remote triangulation from March 2007 to December 2009 (see Plotz, 2014). When locating rhinos, we selected individuals at random without replacement until each of the 14 study animals had been located before selecting again from our rhino cohort (e.g. Plotz *et al.*, 2016). For a direct sighting, we first determined the direction of each rhino's unique radio-transmitter signal from high elevations. The identification of an individual rhino and its location were verified by walking towards the radio signal on foot (signal strength becomes louder as proximity increases) while remaining downwind of the rhino until it was sighted. Radio-triangulation estimates were obtained by an observer taking bearings (i.e. measuring the direction of each rhino's unique radio-transmitter signal) at varying distances from the rhino, from two or more sites at high elevation. A hand-held compass was used to estimate the direction of the rhino's radio-signal to the nearest degree. Positions of direct sighting and triangulation bearing points were determined *via* hand-held GPS units (Garmin e-trex model). All triangulation

location bearings were converted into GPS locations using Locate III software (Nams, 2006), where triangulation bearings less than 60° and greater than 180° apart were excluded from estimates of rhino locations by the software's maximum likelihood estimator because they result in lines that intersect gradually and are known to introduce substantial location estimate error (White & Garrot, 1990).

Quantifying observer influence

To quantify and compare the influence of observers on rhino movement we used remote triangulations to measure daily (24 h) displacement distances after 108 direct sightings during which the rhino was disturbed to varying degrees. Bearings for triangulation data were taken from a median distance of more than a kilometre away (1.5 km) and are, therefore, unlikely to have disturbed rhinos. During visits, two observers were typically < 50 m from the rhinos and remained for ≤ 20 minutes. Median 24 h displacement distances were also estimated by conducting triangulations on study rhinos 24 h before their scheduled visits ($n = 116$ samples). Comparing 24 h displacement distances in this way controlled for errors in the triangulated location estimates. When visited and sighted, each rhino's awareness and response to the observer was scored on an ordinal scale from 0 (unaware of the researchers) to 3 (displaced by the researchers; see Fig. 1 for description; *cf.* Berger & Cunningham, 1995; Göttert, 2011).

Rhinos have a bimodal activity pattern with early morning and late afternoon activity peaks (Goddard, 1967; Kiwia, 1986; Göttert, 2011) that may modify their movement and response to observers. Also, repeated human exposure may have a habituation affect, where rhino react or displace less over time for the same level of disturbance (e.g. Göttert, 2011). Moreover, due to individual differences some rhinos may be more responsive to observer disturbance than others (e.g. Göttert, 2011). In analyses, therefore, active (08:00–10:00, 15:00–18:00) and inactive (10:01–14:59) time periods, the numerical sequence of each sample, and rhino identity, were included as covariates. Disturbance data were square root transformed and then included as the response variable in a linear-mixed effects model run in the package 'lme4' v. 1.1-10 (Bates *et al.*, 2015) using R v.3.2.2 (R Core Team 2016). Rhino identity was included as a random effect. The effect of observer visit, sample order

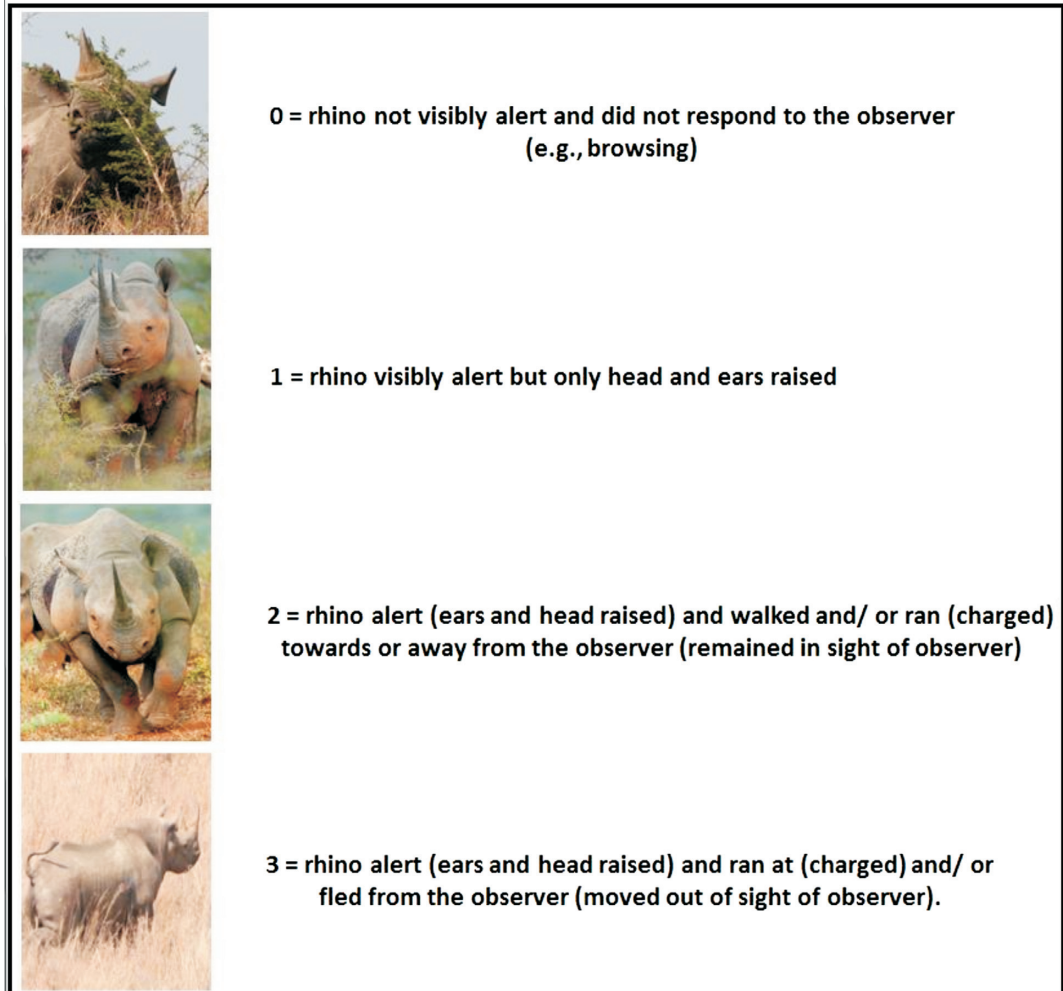


Fig. 1. Illustration depicting the ordinal scale (0 to 3 disturbance score) developed to quantify the level of disturbance rhinos experienced during each observer visit. Photographs by Roan Plotz, Rosalynn Anderson-Lederer and Dale Morris.

(habituation) and time period, on the daily distance travelled by a rhino were assessed by comparing models with and without the term of interest using likelihood ratio tests. For all statistical tests we regarded the critical value (α) of ≤ 0.05 as statistically significant.

Radio-triangulation error

Triangulation error was measured by comparing a black rhino's estimated location by triangulation with a known location obtained from a direct sighting that was conducted immediately after said triangulation. Test data resulted from 72 locations of rhinos first estimated by triangulation and then visually located. The factors known to contribute

the greatest error in triangulation estimates include; the animal's distance from the observer when bearings are taken because greater distances correspond to increased signal refraction, and compound errors in observer interpretation of signal direction (Lee *et al.*, 1985; Schmutz & White, 1990; Saltz, 1994). Also, longer time to complete a triangulation (in this case to also obtain the direct sighting of rhinos), will contribute to differences between the triangulated location and subsequent location when sighted because animals move (Lee *et al.*, 1985; Schmutz & White, 1990). Therefore, we tested the effects of observer bearing distance from a rhino and the typical time researchers would take to complete bearings and

obtain a direct sighting, in a large reserve like HiP, on triangulation error. To accomplish this we collated all triangulated location estimates (calculated using Locate III; Nams, 2006) and direct sighting locations of rhinos and used the Haversine formulae for calculating the shortest distance between two latitude and longitude locations on the earth's surface (Sinnot, 1984).

The recorded positions that observers took bearings from was also collated and the distance between them and corresponding direct sighting (actual) rhino locations was similarly measured to allow observer bearing distance on triangulation error to be tested. For analysing the effect that distance of the bearing point had on the triangulation-estimated *versus* direct-sighting locations, we consistently used the bearing point location (recorded by GPS) taken farthest from the rhino for each triangulation of an individual rhino's location. We also calculated the median point in time between when the first and last triangulation bearing (also for consistency) was completed and the visual sighting of the rhino was obtained, to test the effect that time (i.e. rhino movement) had on triangulation error.

We also predicted there to be a correlation between observers bearing distances from rhinos and the time taken to complete bearings, where greater distances are likely to correspond with longer time periods needed to complete bearings.

The triangulation data were \log_{10} transformed and fitted as the response variables in linear-mixed effects models with rhino identity included as a random effect. The effect of observer distance from the rhino, and the time from triangulation to direct sighting were assessed by comparing models with and without the term of interest using likelihood ratio tests.

The signal strength of radio-transmitters (termed 'gain') has previously been used to assess proximity to black rhinos (e.g. gains of >5.0 associated with distances <234 m from rhino, average 86 m; Linklater & Swaisgood, 2008). The gain can be adequately gauged on the radio-telemetry receiver in 0.1 increments from weaker (e.g. 2) to stronger signal strengths (e.g. ≥ 5), that become stronger as distance to the radio-transmitter (rhino) decreases (Macdonald & Amlaner, 1979; Linklater & Swaisgood, 2008). To illustrate how gain can be used to reduce triangulation error (i.e. reduce distances when taking bearings), we calculated the average gains and observer distances to rhinos associated with our closest, and, for comparison,

farthest, observer distances to rhino when triangulating ($n = 72$ samples each).

RESULTS

Observer influence

The median distance travelled (daily displacement, ± 1 S.E.) by black rhinos during the 24 hours before they were visited by an observer was 1.32 km (IQR = 1.30 km; range = 0.13–4.63 km). In comparison, the same rhino triangulated 24 hours after an observer visit travelled a median of 1.73 km (IQR = 1.76 km; range = 0.14–8.20 km). Visited rhinos were displaced 400 m further than unvisited rhinos but the difference was not statistically significant (LMM: $\chi^2 = 2.11$, $P = 0.15$). There was also no significant effect of sampling order (i.e. habituation: $\chi^2 = 2.10$, $P = 0.15$), or time of day ($\chi^2 = 0.39$, $P = 0.53$) on daily displacement.

Although rhinos that were displaced during observer visits (i.e. disturbance score 3 recorded on 19% of visits, 20/108 samples) moved a median 600 m further on average (2.03 km; IQR = 1.41 km; range = 0.23–8.2 km) compared to unaware rhinos (disturbance score 0 recorded on 48% of visits, 52/108; 1.41 km; IQR = 1.39 km; range = 0.25–4.6 km), this difference was not statistically significant ($\chi^2 = 0.82$, $P = 0.37$; see Fig. 2). Disturbance scores, 1 and 2, indicated that rhinos were visibly

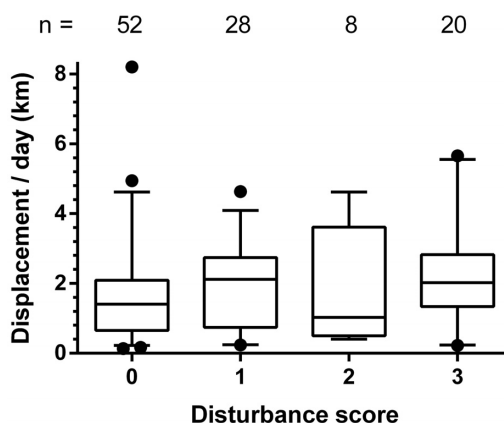


Fig. 2. Mean estimated black rhino displacement distance from 108 triangulated locations 24 hours after an observer visit (disturbance) in Hluhluwe-iMfolozi Park, South Africa. For each observer disturbance event (i.e. direct sighting), each rhino's disturbance response to observers was scored on an ordinal scale from 0 to 3: 0 = rhino not visibly alert and did not respond to the observer, 48%; 1 = rhino alert but only head and ears raised toward observer, 26%; 2 = rhino alert and walked towards or away from the observer, 7%; and 3 = rhino ran from the observer until no longer visible, 19%.

aware of an observer and then walked away, and were recorded on 26% (28/108) and 7% (8/108) of all visits to rhinos, respectively.

Radio-triangulation error

The distance at which farthest triangulation bearings were estimated from rhinos varied from 0.25 to 5.64 km (median of 1.47 km; IQR = 1.54 km). The time taken to complete triangulation bearings varied from 3 to 275 minutes (median of 25 minutes; IQR = 37.75 minutes). The time between triangulation and direct observations of rhinos also varied widely from 7 to 671 minutes (median \pm 1 S.E., 65 minutes; IQR = 133.5 minutes).

Increasing distance of an observer from a rhino when triangulating its location (bearing positions) significantly affected triangulation error (LMM: $\chi^2 = 7.98$, $P < 0.01$; Fig. 3), and was also associated with significantly longer time periods to complete triangulations (i.e. record bearings) ($\chi^2 = 5.61$, $P = 0.02$; Fig. 4) and obtain direct sightings of rhinos, which also significantly affected triangulation error (i.e. rhino movement) ($\chi^2 = 4.28$, $P = 0.04$; Fig. 5).

The median distance between locations estimated by triangulation and actual locations (i.e. discrepancy between locations) was 0.53 km (IQR

0.70 km; range = 0.03–3.8 km). The median farthest observer bearing distances from rhino during triangulations was 1.47 km and was associated with a median gain of 3.5 ± 0.1 (IQR = 0.8; range: 2.5–4.8). Observer's bearing distance from rhinos was reduced by more than a third (0.91 km; IQR = 0.60 km; range: 0.4–3.8 km) when our gain averaged 4.0 ± 0.1 (range: 2.6–5.1) and more than two-thirds (0.49 km; IQR = 0.51 km; range: 0.3–2.1 km) when our gain averaged 4.5 ± 0.1 (range: 3.2–5.2) during bearing measurements.

DISCUSSION

We found small increases in daily displacement distance for black rhinos during a period of regular observer visits (≥ 1 visit every fortnight), including when observers generated escape-responses in rhinos. We found that triangulation error could be substantial and attributable to the distance at which radio-bearings were taken, and animal movement (i.e. time between triangulation and visual sighting of rhino).

Observer influence

Repeated radio-telemetry monitoring of black rhinos that included visiting rhinos for direct observation often resulted in animal disturbance (52%, 56/108, of visits recorded disturbance score 1 to 3,

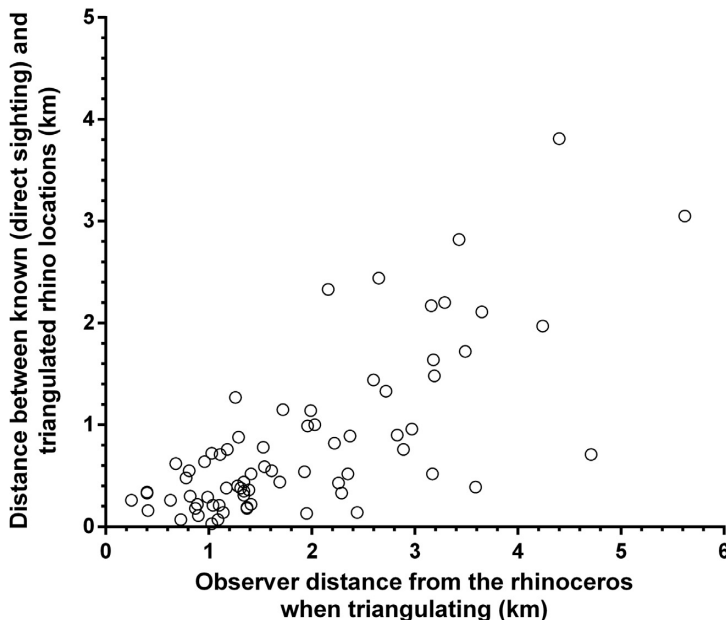


Fig. 3. Trend in discrepancy (km) between locations recorded with triangulation (estimate) and the direct sighting location of black rhinos relative to observer distance from rhino in Hluhluwe-iMfolozi Park, South Africa ($n = 72$ samples).

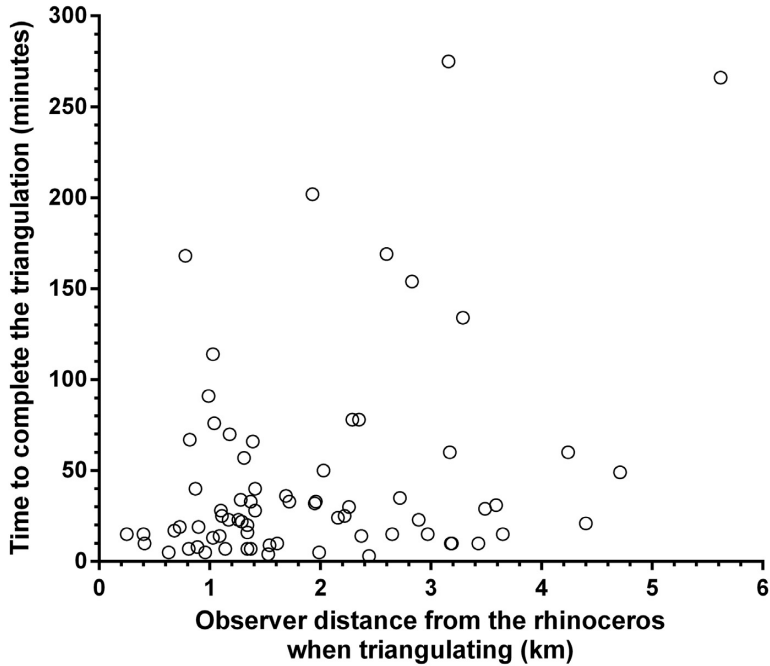


Fig. 4. The time taken to complete triangulation location bearings relative to the distance of the observer from the rhino in Hluhluwe-iMfolozi Park, South Africa ($n = 72$ samples).

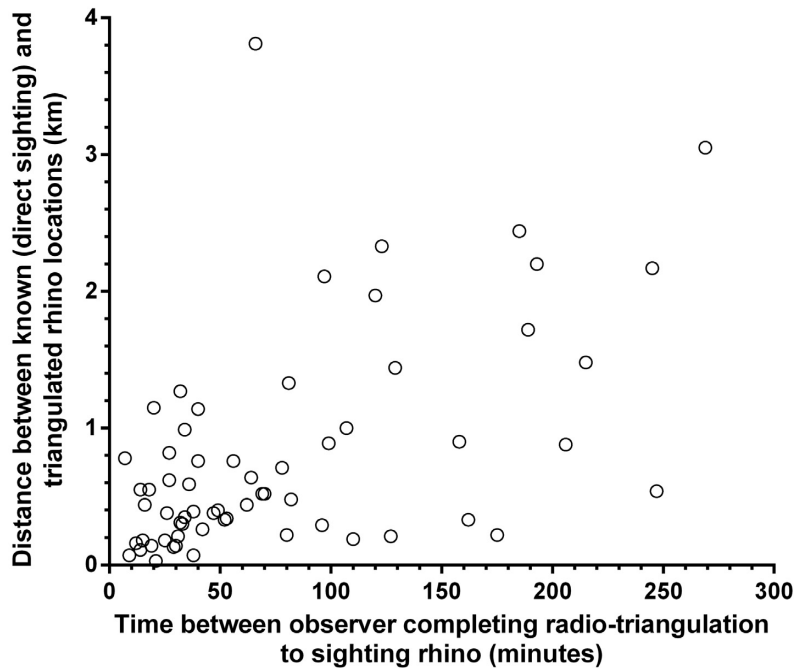


Fig. 5. Trend in discrepancy (km) between locations recorded with triangulation (estimate) and direct sightings of rhinos recorded immediately afterwards ($n = 72$ samples) and relative to the time taken for the observer to complete the triangulation set and directly sight black rhinos in Hluhluwe-iMfolozi Park, South Africa.

see Fig. 1) but this had a small and statistically insignificant effect on their daily displacement distance. Although rhinos moved a median distance of 400 m more during the 24 hours after a visit, they were not displaced sufficiently to substantially alter their location. Indeed, even rhinos that were disturbed and ran from view, did not travel significantly further over the course of 24 hours than rhinos that were recorded as being oblivious of the observer (at least to the end of each visit; Fig. 2). Moreover, rhinos that appeared unaware of the observer during a visit moved a median distance of 1.4 km, similar to the median 1.3 km per day distance travelled by rhinos that had not been visited (i.e. triangulations 24 h before a direct sighting).

Berger & Cunningham (1995) and Beytell (2010), in the only other studies known to quantify black rhino (*D. b. bicornis*) displacement by observers, found them easily disturbed by humans and slow to resume pre-disturbance behaviours. Beytell (2010) recommended human approach distances of no less than 100 m, similar to the recommendations for other taxa. Theuerkauf & Jedrzejewski (2002), for example, recommended that observers tracking wolves (*Canis lupus*) do so from between 200 m and 400 m to reduce their influence on wolf movements. Similar constraints appear unnecessary for HiP black rhinos based on our findings. We found the disturbance created by visiting rhinos to within 50 m for visual identity and location as frequently as once a fortnight to have a limited impact on black rhino movements in HiP. Indeed, our median daily displacement distance after researcher visits for rhinos that fled (± 2.03 km) was half the median human induced displacement distances recorded for black rhinos elsewhere in southern Africa (e.g. c. 4.4 km in Namibia; Berger & Cunningham, 1995). Nevertheless, we recommend that precautionary measures of observers' influence be a standard part of intensive monitoring efforts of rhinos.

Populations may vary in their sensitivity to anthropogenic disturbance and monitoring regimes and observers vary in their propensity to displace wildlife. HiP's rhino population has been annually harvested for over 60 years to assist with a species range expansion programme (i.e. 5–8% of population; Hitchins, Keep & Roach, 1972; Emslie, 2001; Clinning *et al.*, 2009; Plotz, 2014), which may have acclimatized them to regular human disturbance. Moreover, we did not investigate if habitat use (within home range) by rhinos was spatially or

temporally altered by our regular disturbances. In Kenya, for example, wild dogs (*Lycaon pictus*) in human *versus* non-human dominated areas had similar home range sizes, but area-avoidance and intra-species overlaps increased in human dominated areas (Woodroffe, 2011). For rhinos, displacement distance and energetic costs might also have a non-linear relationship where greater distances travelled translate into more or less energy expended. Understanding the relationship between movement and energetic cost for rhinos would improve our understanding of the ecological impacts of disturbance on rhinos. We were, however, unable to equate distance to energetic costs because we have no metric or way of measuring the energetic costs in the field with wild rhinos (e.g. horses, *Equus caballus*; Minetti, Ardigo, Reinach & Saibene, 1999). Nonetheless, the impact of a non-linear relationship between distance and energetic costs is much less likely over the short distances we recorded compared with greater displacement distances wherein the rhino is likely to encounter a greater diversity of terrain or become energetically anaerobic. Incorporating measures of less visible responses by rhinos to human disturbance would also greatly improve assessments of its impact (e.g. heart rate, Nimon, Schroter & Stonehouse, 1995; distress; Linklater *et al.*, 2010b), but again testing this remained outside the scope of our study. Further investigations of black rhino movements, energetic costs and range use at finer scales (including physiological responses; e.g. Linklater *et al.*, 2010b), within human-disturbed habitats are required.

Triangulation error

The median 530 m discrepancy between triangulation-estimated locations and visually confirmed locations of rhinos highlights the amplifying effect that observer distance can have on spatial error when triangulating. Greater observer distance can also amplify the time taken to complete bearings, with a significant positive relationship between triangulation error and time to complete the triangulation. This was probably due to animal movement while the estimate was taking place meaning that observer distance and time to triangulate were both strong explanations of rhino location error.

Ours is the first black rhino study to measure triangulation error. It raises questions about the precision of black rhino home range and habitat-use studies that use substantial numbers of

radio-triangulation estimates without considering (testing) location error (e.g. 81% of all locations in Göttert *et al.*, 2010, were triangulations). Spatial error should be measured and reported and, if necessary and possible, mitigated in home range studies by triangulating closer to the animal.

Theuerkauf & Jedrzejewski (2002) achieved a mean radio-triangulation error of 0.19 km by having 75% of their triangulations on wolves conducted at an observer distance of between 0.20 and 1.2 km. Our results indicate that if observers want to significantly improve the precision of radio-triangulations for black rhinos, they should aim to minimize observer distance from rhino when triangulating. Analysis of our data shows that median triangulation location error is reduced by almost half when bearings are taken from less than 1.0 km from the rhino (e.g. to 0.29 km *cf.* to overall median of 0.54 km). Also, spatial error in triangulated locations is reduced by a similar amount when the time from triangulating to sighting the rhino was completed in under 30 minutes (e.g. to 0.28 km with IQR of 0.43 km *cf.* to overall median of 0.54 km with IQR of 0.70 km).

Our understanding of the spatial ecology of black rhinos are hampered by methodological inconsistencies across location studies and a disregard for sources of location error (Linklater *et al.*, 2010a; Plotz *et al.*, 2016). Accurate location estimates are important because they provide greater insights into the ecological needs and the spatial structure of black rhino populations (e.g. male and female rhino's seasonal movements, Plotz *et al.*, 2016; responses to changing population density, Linklater & Hutcheson, 2010). We recommend, therefore, that researchers in the field aim to significantly reduce triangulation location error for black rhinos by adopting distance protocols when completing individual triangulation bearings, because shorter distances (e.g. preferably <1 km, not >2 km = median 1.33 km discrepancy between triangulated and direct sighting locations, with IQR 1.41 km) reduces the time needed to complete triangulations, which ultimately limits the affect rhino movement has on location error.

To reduce observer distances to decrease overall triangulation error researchers should, whenever possible, aim to record bearings of black rhino locations with gain (signal strength reading) levels of 4 or above (e.g. median observer distance of 0.91 km). The recommendations above are based upon data gathered by observers ($n = 2$) that had several years' experience tracking rhinos. Our

recommendations will likely vary according to the level of experience and/or skill of observers that track black rhinos.

Conservation implications

Researchers and managers monitoring black rhinos will be reassured that direct observations, often causing disturbance and animal displacement, at bi-weekly intervals, had little impact on rhino daily movements. However, triangulation error can lead to substantial errors in animal location data. We recommend that bearings for radio-triangulation of black rhino locations occur from shorter distances and time periods. Nonetheless, more research into rhino socio-spatial ecology is needed to determine whether black rhinos are avoiding human disturbed areas at finer spatial scales (*cf.* wild dogs; Woodroffe, 2001).

Inaccurate, non-standardized location data have the potential to mislead black rhino population management (see Linklater *et al.*, 2010a; Plotz *et al.*, 2016). Thus, assessing and reporting on known errors in radio-telemetry location studies (e.g. Kauhala & Tiilikainen, 2002; Theuerkauf & Jedrzejewski, 2002; Harless, Walde, Delaney, Pater & Hayes, 2010; Gula & Theuerkauf, 2013; Plotz *et al.*, 2016) should become best practice (Macdonald & Amlaner, 1979; Harris *et al.*, 1990; White & Garrott, 1990; Saltz, 1994; Frair *et al.*, 2010). The magnitude of observer disturbance and triangulation error is likely to differ over time, between species, populations and sites. Reporting measures for spatial error, as presented here, would permit the development of objective thresholds for data inclusion (Saltz, 1994; Frair *et al.*, 2010; Gula & Theuerkauf, 2013; Plotz *et al.*, 2016) to improve radio-telemetry data quality and inter-study comparisons (e.g. Laver & Kelly, 2008; Plotz *et al.*, 2016). Refining our understanding of rhino spatial ecology requires radio-telemetry studies to repeatedly test and report on observer effect and triangulation error.

In future, as technology options for monitoring rhinos develop (e.g. drones; Mulero-Pázmány, Stolper, Van Essen, Negro & Sassen, 2014), minimizing or even preventing observer influence and triangulation error will likely become possible. However, under-reporting of known sources of animal disturbance and location error remains an issue across all wildlife monitoring studies, including those that use GPS satellite technology (Frair *et al.*, 2004; Frair *et al.*, 2010). Wildlife managers and researchers would benefit from

more meaningful inter-study comparisons if testing and reporting on known sources of disturbance and location error, relative to the technology used (Frair *et al.*, 2004), became standard practise.

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REFERENCES

- Alibhai, S.K. & Jewell, Z. (2001a). Hot under the collar: the failure of radio-collars on black rhinoceros *Diceros bicornis*. *Oryx*, 35, 284–288.
- Alibhai, S.K. & Jewell, Z. (2001b). Reply to Raoul du Toit. *Oryx*, 35, 291.
- Amin, R., Okita-Ouma, B., Adcock, K., Emslie, R.H., Mulama, M. & Pearce-Kelly, P. (2006). An integrated management system for the conservation of Eastern black rhinoceros *Diceros bicornis michaeli* in Kenya. *International Zoo Year Book*, 40, 118–129.
- Balfour, D.A. & Howison, O. (2001). Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. *African Journal of Range and Forage Science*, 19, 45–53.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
- Beale, C.M. & Monaghan, P. (2004). Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, 41, 335–343.
- Berger, J. & Cunningham, C. (1995). Predation, sensitivity, and sex: why female black rhinoceroses outlive males. *Behavioral Ecology*, 6, 57–64.
- Beytell, P.C. (2010). *Reciprocal impacts of black rhinoceros and community-based ecotourism in North-West Namibia*. (Unpublished M.Sc. thesis). Stellenbosch, South Africa: University of Stellenbosch.
- Brookes, P.M. & MacDonald, I.A.M. (1983). The Hluhluwe-Umfolozi Reserve: an ecological case history. In R. N. Owen-Smith (Ed.), *Management of large mammals in African conservation areas* (pp. 51–78). Pretoria, South Africa: Haum.
- Carey, M.J. (2009). The effects of investigator disturbance on procellariiform seabirds: a review. *New Zealand Journal of Zoology*, 36, 367–377.
- Carney, K.M. & Sydeman, W.J. (1999). A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, 22, 68–79.
- Clinning, G., Druce, D., Robertson, D., Bird, J. & Nxele, B. (2009). *Black rhino in Hluhluwe-Umfolozi Park: historical records, status of current population and monitoring and future management recommendations*. Pietermaritzburg, South Africa: Ezemvelo KwaZulu-Natal Wildlife Report.
- Crosmary, W.-G., Valeix, M., Fritz, H., Madzikanda, H. & Cote, S.D. (2012). African ungulates and their drinking problems: hunting and predation risks constrain access to water. *Animal Behavior*, 83, 145–153.
- Culik, B.M. & Wilson, R.P. (1995). Penguins disturbed by tourists. *Nature*, 376, 301–302.
- Emslie, R. (2001). Black rhino in Hluhluwe-Umfolozi Park. In R.H. Emslie (Ed.), *Southern African Development Community (SADC) rhino management group (RMG) workshop on biological management to meet continental and national black rhino conservation goals* (pp. 86–91). Giants Castle, South Africa: SADC Regional Programme for Rhino Conservation.
- Emslie, R. (2015). *Diceros bicornis*. The IUCN Red List of Threatened Species. Version 2015.2. Retrieved from: www.iucnredlist.org on 20 July 2015.
- Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H., Stenhouse, G.B. & Beyer, H.L. (2004). Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, 41, 201–212.
- Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. (2010). Resolving issues of imprecision and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B*, 365, 2187–2200.
- Frederick, P.C. & Collopy, M.W. (1989). Researcher disturbance in colonies of wading birds: effects of frequency of visit and egg-marking on reproductive parameters. *Colonial Waterbirds*, 12, 152–157.
- Goddard, J. (1967). Home range, behaviour and recruitment rates of two black rhinoceros populations. *East African Wildlife Journal*, 5, 133–150.
- Göttert, T., Schöne, J., Zinner, D., Hodges, J.K. & Böer, M. (2010). Habitat use and spatial organisation of relocated black rhinos in Namibia. *Mammalia*, 74, 35–42.
- Göttert, T. (2011). *On the acclimatisation of African rhinoceros after re-introduction to former livestock farmland in Namibia*. (Unpublished Ph.D. thesis). Hannover, Germany: University of Veterinary Medicine.

- Gula, R. & Theuerkauf, J. (2013). The need for standardization in wildlife science: home range estimators as an example. *European Journal of Wildlife Research*, 59, 713–718.
- Harless, M.L., Walde, A.D., Delaney, D.K., Pater, L.L. & Hayes, W.K. (2010). Sampling considerations for improving home range estimates of desert tortoises: effects of estimator, sampling regime, and sex. *Herpetological Conservation & Biology*, 5, 374–387.
- Harris, S., Cresswell, W.J., Forde, P.G., Trewalla, W.J., Woolard, T. & Wray, S. (1990). Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20, 97–123.
- Hayward, M.W. & Hayward, G.J. (2009). The impact of tourists on lion *Panthera leo* behavior, stress and energetics. *Acta Theriologica*, 54, 219–224.
- Hayward, M.W., Ripple, W.J., Kerley, G.I.H., Landman, M., Plotz, R.D. & Garnett, S.T. (2017). Neocolonial conservation: is moving rhinos to Australia conservation or intellectual property loss? *Conservation Letters*, DOI: 10.1111/conl.12354
- Hitchins, P.M., Keep, M.E. & Roach, K. (1972). The capture of black rhinoceros in Hluhluwe Game Reserve and their translocation to the Kruger National Park. *Lammergeyer*, 17, 18–30.
- Hitchins, P.M. (1990). Census and marking systems for black rhino *Diceros bicornis* with special reference to the Zululand Game Reserves. *The Game Ranger* (December), 1–12.
- Kauhala, K. & Tiilikainen, T. (2002). Radio location error and the estimates of home-range size, movements, and habitat use: a simple field test. *Annales Zoologici Fennici*, 39, 317–324.
- Kiwi, H.Y.D. (1986). Diurnal activity pattern of the black rhino *Diceros bicornis* L. in the Ngorongoro Crater, Tanzania. *African Journal of Ecology*, 24, 89–96.
- Kolowski, J.M. & Holekamp, K.E. (2009). Ecological and anthropogenic influences on space use by spotted hyenas. *Journal of Zoology, London*, 277, 23–36.
- Laver, P.N. & Kelly, M.J. (2008). A critical review of home range studies. *Journal of Wildlife Management*, 72, 290–298.
- Law, P.R. & Linklater, W.L. (2015). Rhinoceros demography should be stage, not age, based. *African Journal of Ecology*, 52, 571–573.
- Lee, J.E., White, G.C., Garrott, R.A., Bartman, R.M. & William-Aldredge, A. (1985). Accessing accuracy of radiotelemetry system for estimating animal locations. *Journal of Wildlife Management*, 4, 658–662.
- Linklater, W. L. & Swaisgood, R.R. (2008). Reserve size, conspecific density, and translocation success for black rhino. *Journal of Wildlife Management*, 72, 1059–1068.
- Linklater, W.L. & Hutcheson, I. (2010). Black rhinoceros are slow to colonize a harvested neighbours range. *South African Journal of Wildlife Research*, 40, 58–63.
- Linklater, W. L., Plotz, R.D., Kerley, G.I.H., Brashares, J.S., Lent, P.C., Cameron, E.Z., Law, P.R. & Hitchins, P.M. (2010a). Dissimilar home range estimates for black rhinoceros *Diceros bicornis* cannot be used to infer habitat change. *Oryx*, 44, 16–18.
- Linklater, W.L., MacDonald, E.A., Flamand, J.R.B. & Czekala, N.M. (2010b). Declining and low fecal corticoids are associated with distress, not acclimation to stress, during the translocation of African rhinoceros. *Animal Conservation*, 13, 104–111.
- Linklater, W.L., Gedir, J., Law, P., Swaisgood, R., Adcock, K., du Preez, P., Knight, M. & Kerley, G.I.H. (2012). Translocations as experiments in the ecological resilience of an asocial mega-herbivore. *PLOS ONE*, 7, e30664.
- Macdonald, D.W. & Amlaner, C.J. (1979). *A practical guide to radio tracking. A handbook on biotelemetry and radio tracking*. Oxford, U.K.: Pergamon Press, 143–159.
- Matson, T.K., Goldizen, A.W. & Putland, D.A. (2005). Factors affecting the vigilance and flight behavior of impalas. *South African Journal of Wildlife Research*, 35, 1–11.
- Minetti, A.E., Ardigo, L.P., Reinach, E. & Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. *Journal of Experimental Biology*, 202, 2329–2338.
- Morgan, S., Mackey, R.L. & Slotow, R. (2009). A priori valuation of land use for the conservation of black rhinoceros *Diceros bicornis*. *Biological Conservation*, 142, 384–393.
- Mulero-Pázmány, M., Stolper, R., Van Essen, L.D., Negro, J.J. & Sassen, T. (2014). Remotely piloted aircraft systems as a rhinoceros anti-poaching tool in Africa. *PLOS ONE*, 9, p.e83873.
- Nams, V. (2006). Locate III software (version 2.0). Tatamagouche, Nova Scotia, Canada: Pacer Computer Software. Retrieved from: <http://www.locateiii.com/Download.htm> on 1 February 2011.
- Nimon, A.J., Schroter, R.C. & Stonehouse, B. (1995). Heart rate of disturbed penguins. *Nature*, 374, 415.
- Odendaal, K. (2011). *Disturbance and habitat factors in a small reserve: home range establishment by black rhino (Diceros bicornis minor)*. (Unpublished M.Sc. thesis). Johannesburg, South Africa: University of the Witwatersrand.
- Odendaal-Holmes, K., Marshal J.P. & Parrini, F. (2014). Disturbance and habitat factors in a small reserve: space use by establishing black rhinoceros (*Diceros bicornis*). *South African Journal of Wildlife Research*, 44, 148–160.
- Owen-Smith, N. (1987). Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 13, 351–362.
- Owen-Smith, N. (1988). *Megaherbivores: the influence of large body size on ecology*. Cambridge, U.K.: Cambridge University Press.
- Pienaar, D. & Hall-Martin, A. (1991). Radio transmitter implants in the horns of both the white and the black rhinoceros in the Kruger National Park. *Koedoe*, 34, 89–96.
- Plotz, R.D. & Linklater, W.L. (2009). Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. *African Zoology*, 44, 283–287.
- Plotz, R.D. (2014). *The interspecific relationships of black rhinoceros (Diceros bicornis) in Hluhluwe-iMfolozi Park*. (Unpublished Ph.D. thesis). Wellington, New Zealand: Victoria University of Wellington.
- Plotz, R.D., Grecian, W.J., Kerley, G.I.H. & Linklater, W.L. (2016). Standardising home range studies for improved

- management of the critically endangered black rhinoceros. *PLOS ONE*, 11(3), e0150571.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from: <http://www.R-project.org/> in February 2017.
- Rodway, M.S., Montevecchi, W.A. & Chardine, J.W. (1996). Effects of investigator disturbance on breeding success of Atlantic puffins. *Biological Conservation*, 76, 311–319.
- Saltz, D. (1994). Reporting error measures in radio location by triangulation: a review. *Journal of Wildlife Management*, 58, 181–184.
- Schenkel, R. & Schenkel-Hulliger, L. (1969). *Ecology and Behaviour of the Black Rhinoceros* (*Diceros bicornis* L.), *Mammalia Depicta* (series). Hamburg & Berlin, Germany: Verlag Paul Parey Scientific Publishers.
- Schmutz, J.A. & White, G.C. (1990). Effects on animal movement on triangulation. *Journal of Wildlife Management*, 54, 506–510.
- Selier, J., Slotow, R. & Di Minin, E. (2015). Large mammal distribution in a transfrontier landscape: trade-offs between resource availability and human disturbance. *Biotropica*, 47, 389–397.
- Senigaglia V., Christiansen F., Bejder L., Gendron D., Lundquist D., Noren D.P., Schaffar A., Smith J.C., Williams R., Martinez E. & Stockin K. (2016). Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance. *Marine Ecology Progress Series*, 19, 251–63.
- Shrader, A. M. & Beauchamp, B. (2001). A new method for implanting radio transmitters into the horns of black and white rhinoceros. *Pachyderm*, 30, 81–86.
- Sinnott, R.W. (1984). Virtues of the haversine. *Sky and Telescope*, 68, 159.
- Theuerkauf, J. & Jedrzejewski, W. (2002). Accuracy of radiotelemetry to estimate wolf activity and locations. *Journal of Wildlife Management*, 66, 859–864.
- Thomas, B., Holland, J.D. & Minot, E.O. (2008). Elephant (*Loxodonta africana*) home ranges in Sabi Sand Reserve and Kruger National Park: a five-year satellite tracking study. *PLOS ONE*, 3, e3902.
- Walker, B.G., Boersma, P.D. & Wingfield, J.C. (2005). Physiological and behavioral differences in magellanic penguin chicks in undisturbed and tourist-visited locations of a colony. *Conservation Biology*, 19, 1571–1577.
- White, G.C. & Garrott, R.A. (1990). *Analysis of radio-tracking data*. New York, U.S.A.: Academic Press.
- Woodroffe, R. (2011). Ranging behavior of African wild dog packs in a human dominated landscape. *Journal of Zoology*, London, 283, 88–97.

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